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Global warming may lower thermal barriers against invasive species in freshwater ecosystems – A study from Lake Constance

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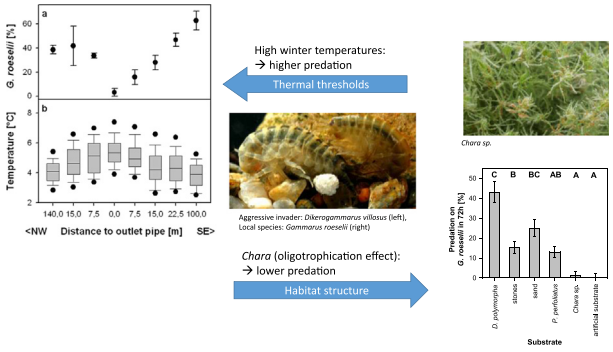
HIGHLIGHTS

- Coexistence between globally successful invader and 'weak' established species
- Low winter temperatures provide thermal shelter.
- Global warming threatens thermal barrier possibly leading to extinction until 2085.

GRAPHICAL ABSTRACT



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ABSTRACT

European freshwater ecosystems are increasingly invaded by exotic animal and plant species. Apart from increased connectivity between previously separated watersheds, the increasing temperature of the hydrosystems favors the spread of exotic species. The freshwater fauna of Central Europe is still shaped by the cold-adapted animal assemblages resulting from the last glaciation. It is less diverse, and the species are putatively less performant competitors, compared to the warm-adapted, species-rich fauna of the Ponto-Caspian realm, from which many current aquatic invaders are coming. Our study analyses potential mechanisms explaining the coexistence between one of the most impacting aquatic invaders of the past decades, the 'killer shrimp' *Dikerogammarus villosus* and the previously dominating amphipod *Gammarus roeselii* in Lake Constance, using laboratory predation experiments and field surveys. Our results indicate two key drivers for coexistence: low winter temperatures and the substrate structure of the alga *Chara* sp. At temperatures below 6 °C, the predation pressure on *G. roeselii* was strongly reduced; *G. roeselii* can therefore disperse throughout the littoral in winter, avoiding predation by *D. villosus*. Artificial heating of a section of the lake shore, however, resulted in local extinction of *G. roeselii* by *D. villosus*. The macroalga *Chara* sp. completely inhibited predation by *D. villosus* on *G. roeselii*. Climate change scenarios indicate that global warming might destroy this thermal refuge during winter until 2085. For the survival of *G. roeselii* it will then be crucial, which part of the *Chara* population will maintain epigeic plant parts during winter. The complex interplay between thermal and physical refuges for native species in the context of climate change and changing trophic status of freshwater systems, as disentangled by our study, shows that ecosystem management and restoration strategies need to better consider multiple stressors (and their rather complex mitigation strategies).

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1. Introduction

Biological invasions occur more and more often, and their global economic effect often exceeds the effects of environmental pollution (Lövei, 1997; Vitousek et al., 1997). Invasive species have been identified as one of the major threats of freshwater ecosystems in the last decades (Sala et al., 2000). Even single species invasions can change entire ecosystems such as the introduction of the Ponto-Caspian mussel *Dreissena polymorpha* in the Great Lakes in North America (e.g. Ludyanskiy et al., 1993; Ward, 1985). Many factors influence the success of freshwater invaders, e.g. homogenization of habitat structures, weakening of the native assemblages by pollution, 'invasional meltdown' by mutual subsidies from different invasive species, and diseases and parasites brought by the invaders, which are new to the native species (Keller et al., 2011; Leuven et al., 2009). The synchrony of improved water quality and increased temperature trends, currently found in many European water systems, may provoke confounding effects in freshwater invertebrate assemblages (Floury et al., 2013).

Climate change is known to influence natural communities (e.g., Urban et al., 2016), but it can also increase the impact of invasive aquatic species, e.g. their competitive and predatory effects on native species, or the virulence of some diseases, thus requiring new prevention and control strategies (Rahel and Olden, 2008). Climate change also affects aquatic ecosystem processes, e.g. by changing discharge regimes including prolonged droughts and ephemerisation of previously running waters, or by producing heat waves. Those may act as "windows of opportunity" for the establishment of invasive species, including parasites, such as the mass development of the "swimmer's itch", *Trichobilharzia franki*, in Lake Constance during the heat wave in summer 2003 (Fiedler et al., 2005). In our study, we focus on the effects of increasing water temperature on the success of a recent invader (*Dikerogammarus villosus*), which has caused considerable changes in the benthic invertebrate assemblages in Europe.

European freshwater ecosystems are recently heating up due to Climate Change and inflowing cooling or waste water. For example, long sections of the River Rhine hardly ever cool below 5 °C in winter (Schöll, 2000). A recent study on 475 sites in seven river basins of Germany has revealed a mean warming trend of 0.03 °C year^{-1} during the 1985–2010 period (Arora et al., 2016), the Loire River has increased approximately 0.8 °C year^{-1} (Moatar and Gailhard, 2006); prealpine lakes (Lake Constance, Lake Zurich) have been increasing by 0.021–0.054 and Lake Stensjön (Sweden) as much as 0.157 °C year^{-1} during the 1970–2008 period (Adrian et al., 2009).

Considering the biogeographical situation of Central Europe, these temperature trends are specifically worrying because its freshwater fauna derives in large parts from glacial relics (i.e. cold-stenothermous species) and the post-glacial recolonization by natural dispersal has been relatively slow, because river and lake ecosystems have been separated from their southern and south-eastern correlates by basin divides acting as geographical barriers (Dehling et al., 2010; Illies, 1978). The increased passability of these barriers due to canal construction (specifically the canal connecting the Rhine and Danube basins) and reduced environmental quality (water pollution, habitat degradation), combined with the increased water temperatures represent a scenario that is very favorable for a fast colonization of central European hydrosystems such as the Rhine river by non-native species (Beisel et al., 2017). Higher temperatures generally seem to increase the success of thermophilous, ponto-caspian invaders in Central Europe (Fruh et al., 2012; Gergs and Rothhaupt, 2015) but at the upper thermal limit (temperatures above 25 °C), alien freshwater crustaceans do not seem to perform better than their local congeners (Maazouzi et al., 2011, Verberk et al., 2018 and literature therein). Low water temperatures during winter may represent a thermal barrier for the thermophilic invaders and a temporal "window of opportunity" for the native fauna to survive. For example, populations of the invasive Asian clam *Corbicula fluminea* became considerably reduced during the cold winter 2012/13 in the Loire River (Wantzen and Richard, 2016). Global warming, however, may break down these thermal barriers.

One of the most alarming invasive freshwater invertebrate species in Europe is the amphipod *Dikerogammarus villosus*. In the past decades, it spread through most of the continent and displaced nearly all native amphipods in waterways (e.g. Bij de Vaate et al., 2002; van der Velde et al., 2000; van Riel et al., 2006). In the Rhine River it has even outcompeted *Gammarus tigrinus*, which originated in North America and had displaced many European amphipods years before (Haas et al., 2002). Several behavioral and physiological features make *D. villosus* a "perfect invader" (Rewicz et al., 2014). Compared with other gammarids, it displays a high fecundity, early maturity, fast growth and co-occurrence of up to 14 cohorts at a time (Pöckl, 2007; Pöckl, 2009; Wijnhoven et al., 2003), low metabolic rates and high glycogen reserves (Becker et al., 2016; Maazouzi et al., 2011), an energy-efficient and temperature-adapted preying strategy (Pellan et al., 2015), high salinity tolerance (Piscart et al., 2011) and excellent spreading mechanisms (Bacela-Spychalska et al., 2013). The main displacement mechanism, however, seems to be intraguild predation on other amphipods, as described by Dick et al. (2002). Due to this high invasional potential *D. villosus* can be regarded as a global threat, e.g., for North American freshwater ecosystems such as the Great Lakes system (Bruijs et al., 2001). *D. villosus* is a less performant shredder than native amphipods such as *G. fossarum* or *G. roeselii*, thus a complete replacement of the native amphipods may have negative impacts on the organic matter budgets of lake ecosystems, whereas under coexistence, leaf litter breakdown rates could remain reasonably high (Little and Altermatt, 2018).

D. villosus was first recorded in Lake Constance in 2003 (Mürle et al., 2004) and quickly spread throughout the lake (Hesselschwerdt et al., 2008). Lake Constance is the second largest prealpine lake. Large parts of its water arrive from the alpine Rhine catchment, and it flows into the Rhine River further downstream (Uehlinger et al., 2009). Due to the Rhine fall at Schaffhausen, there is no navigable connection between the water bodies, thus Lake Constance (bordered by Germany, Switzerland, and Austria) lacks many of the invasive species that inhabit the river, however, some invasive species have found their way into the lake, such as *Dreissena polymorpha, Corbicula fluminea* and diverse benthic-pelagic shrimp species (Gergs and Rothhaupt, 2015; Hanselmann et al., 2013; Mörtl and Rothhaupt, 2003; Rothhaupt et al., 2014; Werner et al., 2005; Werner and Rothhaupt, 2007).

Before the arrival of *D. villosus* in Lake Constance, its amphipod communities had already undergone changes. The earliest recorded recent species are *Gammarus fossarum*, *G. lacustris* and *G. pulex* (Muckle, 1942; Schellenberg, 1942). Later, *Gammarus roeselii* (Gervais) appeared in Lake Constance. This species, originating from the Balkans (Jazdzewski, 1980), was first recorded in Central Europe near Paris (Gervais, 1835), however it is not considered a strong competitor to the native invertebrate fauna (Josens et al., 2005). In the past decades, fostered by the eutrophic phase of Lake Constance (1960s to 1980s), *G. roeselii* was dominating, but its densities strongly declined after the invasion of *D. villosus* (Mörtl et al., 2005), most likely due to direct predation by *D. villosus* (Hesselschwerdt et al., 2009; Kinzler and Maier, 2003), or source competition (Rothhaupt et al., 2014). Currently, the density of *D. villosus* determines 26% of the variability of benthic invertebrate assemblages in Lake Constance (Gergs and Rothhaupt, 2015).

In spite of these findings, both amphipod species coexisted in plant parts of the macroalga *Chara* sp. and in winter, and *G. roeselii* even dominated parts of the littoral (Hesselschwerdt et al., 2008). In order to test hypotheses for this coexistence, different laboratory studies were made. We could show that *G. roeselii* was able to smell and avoid the scent of *D. villosus* (Hesselschwerdt et al., 2009), moreover, slightly different substrate preferences exist (Hesselschwerdt et al., 2008). Further studies tested tolerance against ammonia (Gergs et al., 2013) or pesticides (Bundschuh et al., 2013), both with limited results. Another study had shown that *D. villosus* is able to drive native gammarid species out of

their natural habitats (Kley et al., 2009), therefore, the substrate effect may not have accounted for the coexistence under natural conditions. Moreover, epigeic plant parts of *Chara* sp. generally decompose in Lake Constance during winter (Richter and Gross, 2013), thus its habitat structure alone cannot account for the previously observed coexistence during winter time.

We therefore hypothesized alternating causes for coexistence of the two gammarid species, being the complex habitat structures of *Chara* sp. algae during summer and low temperatures during winter. Both factors were tested in combined laboratory and field studies. The warm water outlet of a thermal bath at city of Constance gave us a rare opportunity to test temperature effects under natural conditions.

To investigate the coexistence of the amphipods, we first performed laboratory experiments to analyze the effect of all common substrates of Lake Constance on predation by *D. villosus* on *G. roeselii*. In order to validate the results of the laboratory experiment, we then measured the densities of the two amphipods on the most common substrates settled by amphipods in the lake. In addition, we tested the influence of temperature as the most important abiotic factor on the competitors during winter, both in laboratory and field experiments. The aim of this study was to provide scientific baselines for an adapted aquatic habitat management scheme under climate change conditions.

2. Materials and methods

2.1. Substrate effects – laboratory experiments

Laboratory experiments were carried out in plastic tanks (40 × 20 × 25 cm) filled with 7 l lake water that had been passed through a 40 μm mesh. The conductivity of the lake water was 304 μS cm^{-1}, the calcium content was 45 mg l^{-1}, and the magnesium content was 7.5 mg l^{-1}. The tanks were placed in a climate chamber at 16 °C under long-day light conditions (14 h light/10 h dark). To assure a natural behavior of *D. villosus* and *G. roeselii*, all individuals were replaced after 7 days with individuals freshly collected from the littoral zone near Konstanz, Germany. *D. villosus* individuals, but not those of *G. roeselii*, were separated according to sex; the sex of *G. roeselii* can only be determined with dead individuals. Care was taken that all animals had approximatively the same size and maturation state considering moulting, freshly moulted animals were not used for experimentation. The mean carapax length of *G. roeselii*, *D. villosus* males, and *D. villosus* females was 7.17 ± 0.72, 9.00 ± 1.09, and 7.99 ± 1.40 mm, respectively. The amphipods were kept in 20-l flow-through systems flushed with filtered lake water and fed every second day with artificial fish food (TetraMin®). All individuals were starved 24 h prior to the experiments.

The percentual loss of individuals in 72 h owing to intra- or interspecific effects was recorded. To determine interspecific predation rates, 10 inter-molt individuals of each species (5 males and 5 females for *D. villosus*) were placed in each tank for 72 h. Cannibalism rates were determined using 10 inter-molt individuals of only one species. Each of these experiments was replicated ten times. To obtain the interspecific predation rates without cannibalistic effects and natural mortality, the cannibalism rates were subtracted from the loss rates in the interspecific predation experiment (Hesselschwerdt et al., 2009).

We tested the cannibalism and interspecific predation rates of *D. villosus* and *G. roeselii* on six different substrate types. Three substrates represented commonly occurring sediment structures in Lake Constance: a) four round stones (∅ 10 cm) each covered with approximately 150 living *Dreissena polymorpha* (Bivalvia) (13 ± 3 mm shell length), b) four bare round stones (∅ 10 cm), and c) a 2-cm layer of sand (∅ <0.2 mm). Two substrates represented the most common macrophytes in the lake, and one artificial substrate simulated the structure of *Chara* sp.: d) seven *Potamogeton perfoliatus* (angiosperm) shoots (10 cm length), e) a 3-cm thick layer of cleaned *Chara* sp. (macro algae) (27.6 ± 5.2 g dry wt.), and f) a 3-cm layer of 0.5 m^2 wadded nylon-netting (4 mm mesh size, twine No. 210/6, knotless, green, obtained from Engel-Netze, Germany) in order to mimic the complex structure of *Chara* sp. The macrophytes and the artificial substrate were placed on a 2-cm layer of sand. All experiments were carried out in summer/autumn 2005 and 2007. To verify the comparability of the results of the two periods, the experiment testing round stones covered with *D. polymorpha* (a) was repeated in 2005 and 2007 and showed very similar results (see below, Section 2.5).

2.2. Substrate effects – field data

Densities of both amphipod species on the most prevalent substrates of Lake Constance for amphipods, i.e., stones covered with *D. polymorpha* (at 2.0 m depth) and *Chara* sp. of that year on sand (at 2.7 m depth) were analyzed in the field in June 2008. Additionally, we sampled the overwintered layer of *Chara* sp. (3.5 m depth); *Chara* sp. does not overwinter every year. The samples were collected by scuba divers in the littoral zone near Konstanz using an infralittoral suction sampler (Baumgärtner, 2004) in an area of 625 cm^2. All amphipods were counted (ind. m^{-2}) and separated into four size classes (<7, 7–11.9, 12–19.9, and ≥20 mm).

2.3. Temperature effects – laboratory experiment

To analyze the influence of water temperature on the interspecific predation rate of *D. villosus* on *G. roeselii*, we used the same setup as described in Section 2.1, including subtraction of cannibalism rate controls. As substrate, we used four bare stones in each experiment. We tested the predation rate at five temperatures (4, 6, 8, 12, and 16 °C) in climate chambers. All experiments and controls were replicated seven times.

2.4. Temperature effects – field data

Amphipod densities in the temperature gradient around the warm water outlet of the thermal bath of the city of Konstanz were analyzed in February 2009. All samples were collected with the infralittoral suction sampler at a depth of 0.3 m as described in Section 2.2. The sampling sites were 7.5, 15.0, and 140 m northwest and 7.5, 15.0, 22.5, and 100 m southeast of the water outlet. All sites had the same gravel substrate and slope, except the most northwestern site, which had a lower inclination than the other sites. The warm water is not directly fed into the lake, rather it is poured onto the gravel bar half a meter above the waterline. When it enters the lake, it is already well mixed with the interstitial water inside the gravel bar and is distributed over several meters along the shoreline. The temperature at all sites and in the outlet pipe was logged hourly from January to March 2009 using TinyTag data loggers. For the statistical analyses, we used the temperature data from the week before the sampling.

2.5. Statistical analyses

The substrate-dependent effects of the predation experiments were analyzed using nonparametric tests due to lacking homogeneity of variance between the different substrates. For all other predation effects the percentage values were root-transformed with $x' = \sqrt[3]{x}$. All associated averages are given as arithmetic mean with standard error. Since we found no difference in the interspecific predation rates on *G. roeselii* on stones between 2005 (16.0% ± 2.6 s.e.) and 2007 (14.3% ± 3.3 s.e.) ($p = 0.607$; $t = 0.524$; $n = 20$; *t*-test), data of both years were pooled. For all statistical analyses, the program SPSS 16.0.1 was used.

2.5.1. Substrate – cannibalism

Cannibalism was verified with one sample *t*-test of the pooled data over all substrates against zero loss. An interspecific difference in

cannibalism rates was tested between the pooled rates of each species using a *t*-test. The influence of the substrate type on the cannibalism rates of both species was analyzed with Kruskal Wallis H-test and Nemenyi post-hoc test.

2.5.2. Substrate – interspecific predation

To detect interspecific predation pressure, we tested the pooled predation rates on each single species over all substrates with one sample *t*-test against zero predation. Since no predation by *G. roeselii* on *D. villosus* was found, this feature was not further analyzed. The substrate dependence of the interspecific predation rates on *G. roeselii* was analyzed with Kruskal Wallis H-test and Nemenyi post-hoc test.

2.5.3. Substrate – field data

Since *G. roeselii* is generally smaller than *D. villosus*, a statistical comparison of the size class distribution between the two species was not reasonable. Instead, total densities of each species were analyzed. All density values were transformed using $x' = \log(x + 1)$ to obtain homogenous variances. Densities on all substrates were compared using one-way ANOVA and Student-Newman-Keuls post-hoc range test for each species separately.

2.5.4. Temperature – laboratory experiments

The temperature dependence of interspecific predation by *D. villosus* on *G. roeselii* and cannibalism rates of each species were each tested with Kruskal Wallis H-test and Nemenyi post-hoc test.

2.5.5. Temperature – field data

The correlation between the median water temperature and the percentage of *G. roeselii* among the amphipods at the different sampling sites was analyzed using the Pearson correlation after angular transformation ($x' = \sqrt{\arcsin(x)}; 0 \le x \le 1$).

3. Results

3.1. Substrate effects – laboratory experiments

3.1.1. Cannibalism

Both amphipod species displayed cannibalistic behavior (Fig. 1a). In 72 h, *D. villosus* reduced the number of conspecifics by 8.67% (±1.18% s.e., $p < 0.001$, $t = 7.371$, $df = 59$, one sample *t*-test), and *G. roeselii* devoured 4.50% (±0.73% s.e., $p < 0.001$, $t = 6.167$, $df = 59$, one sample *t*-test). Intraspecific loss rates differed significantly, i.e., cannibalism in *D. villosus* was higher than in *G. roeselii* ($p = 0.003$, $t = 4.167$, $df = 118$, *t*-test). No substrate-dependent influences on cannibalism rates were found for either species (*D. villosus*: $p = 0.238$, $Chi^2 = 6.775$, $df = 5$; *G. roeselii*: $p = 0.119$, $Chi^2 = 8.751$, $df = 5$, Kruskal Wallis H-test).

3.1.2. Interspecific predation

We observed strong interspecific predation pressure of *D. villosus* on *G. roeselii*. On average, 16.33% (±2.31% s.e.) of *G. roeselii* individuals were eaten by *D. villosus* in 72 h (Fig. 1b; $p < 0.001$, $t = 7.061$, $df = 59$, one sample *t*-test over all treatments). In contrast, we could not detect any interspecific predation pressure of *G. roeselii* on *D. villosus*. In the presence of *G. roeselii*, the loss of conspecifics of *D. villosus* was even lower than the loss through cannibalism in the controls (−2.50% ± 0.89 s.e.) (Fig. 1b; $p < 0.007$, $t = -2.809$, $n = 70$, one sample *t*-test), which accounts for the negative values in Fig. 1. *D. villosus* most likely does not need to feed on conspecifics after feeding on *G. roeselii*.

The analyzed substrates had a strong influence on the predation by *D. villosus* on *G. roeselii*. No predation was found on *Chara* sp. and on the artificial substrate mimicking its structure, very high predation occurred on stones covered with *D. polymorpha*, and intermediate predation occurred on all other substrates (Fig. 1b; $p < 0.001$, $Chi^2 = 42.701$, $df = 5$, Kruskal Wallis H-test, Nemenyi post hoc test).

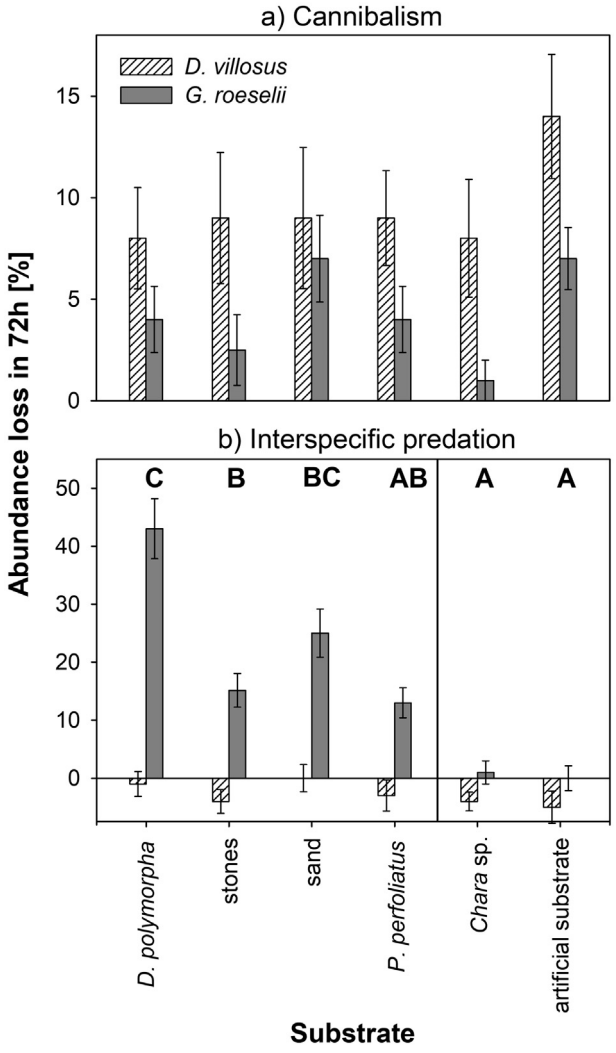

Fig. 1. Substrate-dependent rates of a) cannibalism and b) interspecific predation on *D. villosus* and *G. roeselii*. Bold letters indicate statistically different groups (Kruskal Wallis H-test, Nemenyi post-hoc; mean ± s.e.). Negative abundance losses may occur due to the subtraction of the cannibalism rate.

3.2. Substrate effects – field data

The distribution patterns in the field differed between the two species. *D. villosus* focused on the areas containing *D. polymorpha* (Fig. 2a; $p = 0.019$, $F_{2,12} = 6.317$, one-way ANOVA, SNK post-hoc range test). In contrast, *G. roeselii* avoided *D. polymorpha* and inhabited nearly exclusively stands of *Chara* sp. (Fig. 2b; $p = 0.005$, $F_{2,12} = 10.232$, one-way ANOVA, SNK post-hoc range test).

3.3. Temperature effects – laboratory experiment

The interspecific predation by *D. villosus* on *G. roeselii* was highly influenced by temperature (Fig. 3; $p = 0.013$, $Chi^2 = 12.610$, $df = 4$, Kruskal Wallis H-test, Nemenyi post-hoc test). The predation rates at water temperatures of 8 to 16 °C were comparable to those in the substrate experiments. At 6 °C, the predation rates were lower, and at 4 °C, the rates were nearly zero (Fig. 3). The cannibalism rates of both species were not affected by temperature (*D. villosus*: $p = 0.933$, $Chi^2 = 0.839$, $df = 4$; *G. roeselii*: $p = 0.988$, $Chi^2 = 0.330$, $df = 4$, Kruskal Wallis H-test).

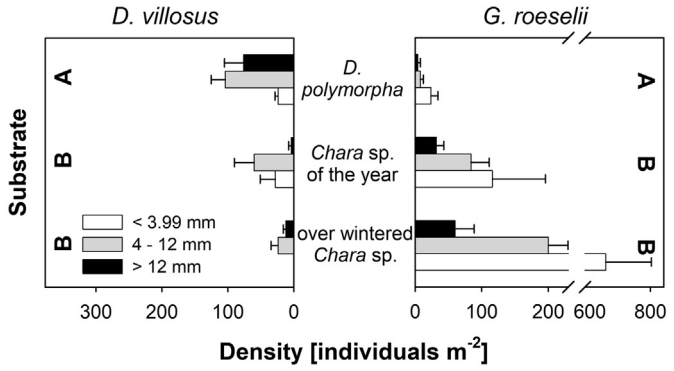

Fig. 2. Densities of a) *D. villosus* and b) *G. roeselii* on different substrates in the littoral zone of Lake Constance. Bold letters indicate statistically different groups (one-way ANOVA, SNK post-hoc range test; mean ± s.e.).

3.4. Temperature effects – field data

The composition of the amphipod community was strongly dominated by *D. villosus* at higher temperatures. The percentage of *G. roeselii* was highly negatively correlated with the median temperature at the corresponding sampling site (Fig. 4; $p = 0.001$, $r = -0.705$, Pearson correlation).

Next to the water outlet, *G. roeselii* was almost completely displaced by *D. villosus*. At this location, the temperature at 0.3 m depth was on average 5.45 °C (+0.61/−0.72; maximum 9.96 °C) owing to mixing with interstitial water in the gravel bed at the shore. However, with growing distance to this warm zone, and at lower temperatures, the relative abundance of *G. roeselii* in relation to *D. villosus* rose to 62% at 100 m SE distance from the outlet (Fig. 4). The median temperature of the water outlet itself was 19.09 °C (+0.86/−5.05; maximum 29.95 °C).

4. Discussion

Overlapping effects of direct and indirect human impacts interacting with natural processes influence aquatic ecosystems at an unprecedented speed, resulting in a serious decline of freshwater biodiversity worldwide (Dudgeon et al., 2006). In the case of the River Rhine basin, invasive species are quickly succeeding one to another, some of which reach Lake Constance. Additionally, the lake undergoes strong changes in water temperature due to Global Warming and in declining phosphate concentrations due to waste water treatment, after having been

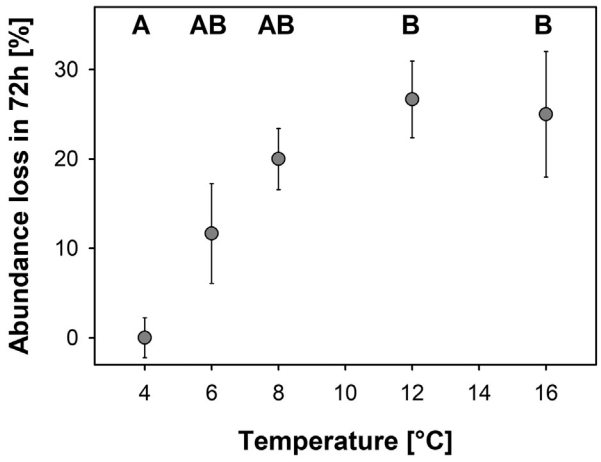

Fig. 3. Influence of temperature on interspecific predation rates of *D. villosus* on *G. roeselii*. Bold letters indicate statistically different groups (Kruskal Wallis H-test, Nemenyi post-hoc; mean ± s.e.).

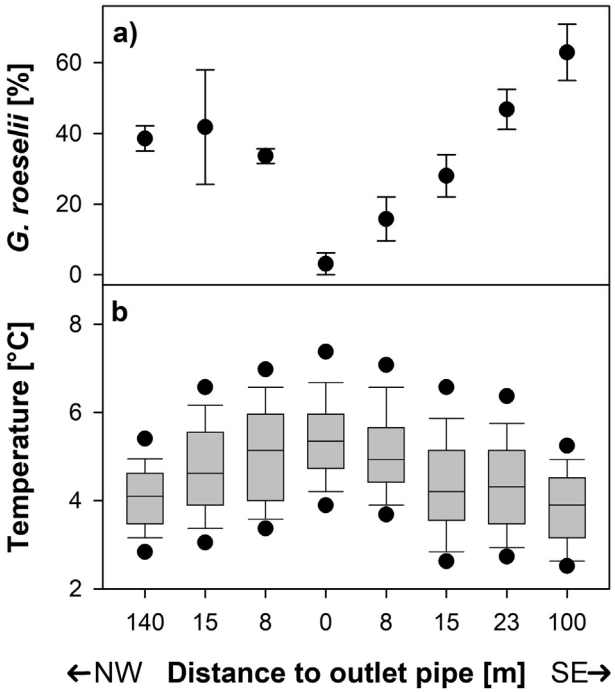

Fig. 4. Influence of thermal loading caused by the warm water outlet of a thermal bath on a) the percentage of *G. roeselii* among *D. villosus* (mean ± s.e.) and b) the temperature along the nearby coast (median with 5, 10, 25, 75, 90 and 95th percentile).

one of the most polluted prealpine lakes in the 1970s. As a consequence of these trends, the biodiversity of the lake changes quickly, especially that of invertebrate assemblages, aquatic macrophytes, and fish communities (Adrian et al., 2009; Gerdeaux et al., 2006; Jeppesen et al., 2005; Richter and Gross, 2013). The arrival of specifically competitive invaders such as *D. villosus* results in a dramatic change of species assemblages, food web structures, and functions of an entire ecosystem. Recently, further exotic species, such as the quagga mussel or benthic-pelagic shrimps have arrived, other species may follow in the future. To mitigate negative effects of an invader, it is important to know which factors may possibly control it, and how environmental management can contribute to this. Our study aimed to contribute answers to these questions.

We could show that *Chara* sp. algae sustained coexistence of the two gammarid species. *D. villosus* may chase out other invertebrate species from their preferred substrates (Kley et al., 2009), but it was not able to do so in the alga or in the artificial substrate mimicking its habitat structure, although both *D. villosus* and *G. roeselii* were found deep inside both substrates throughout the experiments. This suggests that the invader is physically hampered by the habitat structure *Chara* sp. The larger size of *D. villosus* and its farther-protruding peraepods III to V compared to those of *G. roeselii* (Eggers and Martens, 2001) could cause *D. villosus* to move more slowly within the algae than *G. roeselii*, thereby providing *G. roeselii* a chance for escape. On the other hand, vascular macrophytes typical of the meso-eutrophic phase of Lake Constance (e.g., Potamogetonaceae) did not provide sufficient physical shelter for *G. roeselii* (Hesselschwerdt et al., 2008).

Charophytes have been the typical macrophyte vegetation in Lake Constance in the early 20th century (Lauterborn, 1941), however due to high, man-made phosphate loads in Lake Constance in the 1960s to 1980s (up to nearly 90 μg l^{-1}) they suffered a strong dieback during that period and were first replaced by filamentous algae (Schmieder, 2004; Schmieder et al., 2006). As a consequence of intensive wastewater treatment in the lake, there was an intermediary phase of intensive growth of eutraphent macrophytes such as diverse Potamogetonaceae and *Myriophyllum spicatum* (Gross and Kornijow, 2002). Following further reoligotrophication, charophytes have begun to reconquer Lake

Constance in the late 1980s, replacing the more nutrient-demanding macrophytes (Richter and Gross, 2013). Moreover, there is an increasing tendency that *Chara* sp. stands do not die back entirely during winter (J.H. pers. obs. by SCUBA, 2005–2018) but remain until next spring, when they become overgrown by their new shoots. We observed much higher densities of *G. roeselii* (particularly of small juveniles) in overwintered *Chara* sp. than in *Chara* sp. of the year, probably due to the higher structural diversity of the older plants. Reoligotrophication by improved waste water treatment therefore appears to be an important tool to foster plant species that provide refuge habitats such as Characeae, needing oligotrophic conditions. However, there is a current political debate about re-increasing the phosphate concentration in perialpine lakes for the sake of local fisheries (Gerdeaux et al., 2006).

Our field and laboratory results have also evidenced a strongly reduced interspecific predation pressure by *D. villosus* at temperatures below 6 °C. At 5.5 °C and above, *G. roeselii* was nearly completely displaced, but lower temperatures allow a thermal advantage of the permanently active *G. roeselii* over the more energy-efficient sit-and-wait predator *D. villosus*, which continued to feed on chironomid larvae but ceased to prey upon *G. roeselii*. On an average from 2000 to 2017, the mean daily water temperature of Lake Constance at 0.5 m depth near Bregenz remained below 6 °C for 82.3 days (±18.7 days s.d.) from mid-December to mid-March (51.6 ± 24.3 days below 5 °C; 26.6 ± 19.8 days below 4 °C; data provided by Wasserwirtschaft Vorarlberg). Thus, the temperature remains below 6 °C and the predation pressure was reduced during the entire period when *Chara* sp. was scarce or lacking in the littoral zone; in most of the years the winter temperature was even below 4 °C for at least 4 weeks and probably no predation from *G. villosus* occurred at all.

Recent modelling for Lake Constance predicts a rise in epilimnion temperature of 1.6–2.4 °C until 2085 (IGKB, 2015). This will result in much shorter periods of water temperatures <6 °C than today. If we suppose that the littoral will display a similar temperature pattern as the modelled epilimnion, only about 27 days on average will remain below 6 °C (today, 82.3 days remain <6 °C) and it can be doubted that *G. roeselii* will survive at these temperatures without *Chara* sp. The modelling also predicted that in individual years, epilimnion temperatures may not decline to 4 °C at all, which would have severe impacts on the lake stratigraphy and on the survival of *G. roeselii*. The thermal threshold values for the survival of the cold-stenothermous native fauna in the presence of invaders may vary between species and be subject to overlapping effects with other (multiple) stressors, but the general trend towards a rapid change of the faunal assemblages is obvious. There is a clear global trend of lake warming (Sharma et al., 2015), specifically in Lake Constance (Jacob et al., 2008; KLIWA, 2006; Peeters et al., 2007). This may not only cause asynchronous changes in phenology between interacting species (Straile et al., 2015) but it may destroy thermal refuges of local species against impacts from invasive species. These long-term studies corroborate recent trends showing a faster increase of water temperatures than ever recorded.

In conclusion, we could show that two alternating refuges from predation by *D. villosus* exist for *G. roeselii* in Lake Constance: during vegetation growth *Chara* sp. provides physical shelter, and during winter time, low temperatures provide a thermal refuge. Both of these types of refuge are sensitive to human impact. While in our case study, the physical shelter depends on the trophic state of the lake, the thermal refuge is subject to global warming and further warm-water inflows. Regarding the ability of a native species to withstand outcompetition by invasive thermophilous species we make a plea for controlling thermal inputs and for considering refugial habitats of native species as a target for restoration of lake and river ecosystems. Urban heat islands (Grimm et al., 2008) affect terrestrial and aquatic ecosystems alike, they may interrupt connectivity for thermo-sensitive species but they also may create biotic hots spots and hot moments (Wantzen and Junk, 2006) for thermophilous species. Solid substrate structures such as bridge pillars and canals are specifically appropriate to a range of freshwater invaders and serve as refuges for thermophilous invaders, from where their populations become "re-seeded" after cold winter phases. This was observed, among others, for the fast recolonization of the Loire River by *Corbicula* mussels after the cold winter 2012/13 (Wantzen and Richard, 2016). Urban freshwater habitat management should consider this problem by providing heat dissipation structures that reduce the temperature of thermal inlets and by providing more dynamic habitat structures by ecological restoration and environmental flow management.

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